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LINGULA (LINGULIDAE, BRACHIOPODA) FROM THE LATE ARTINSKIAN (PERMIAN), CARNARVON BASIN, WESTERN AUSTRALIA

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Abstract: *Lingula occidentaustralis* sp. nov. is described from the Early Permian Quinnanie Shale of the Carnarvon Basin, Western Australia. Faunal and lithological evidence indicates that the Quinnanie Shale was deposited in a very shallow marine (probably tidal flat) environment. Environmental constraints and global palaeogeography of Permian lingulids indicate that they were at times more tolerant of cooler water than living members of the family. Lingulids appear to have become more specialised and restricted ecologically during the late Palaeozoic.

INTRODUCTION

Occurrence of the inarticulate brachiopod *Lingula* Bruguiere in the Permian succession of the Carnarvon Basin, Western Australia, was first mentioned by Teichert (1939, p. 6), but the species has never been figured or described. The comprehensive review of the family Lingulidae (Rowell 1965) and the recent ecological and taxonomic analysis of Triassic to Recent members of the family (Emig *et al.* 1978) provide an excellent framework for investigation of Palaeozoic lingulids. Taxonomy, ecology and global palaeogeography of Permian representatives of the family are reviewed below.

WESTERN AUSTRALIAN MATERIAL

Stratigraphic Occurrence

In the Permian succession of the Carnarvon Basin *Lingula* is, apparently, restricted to the Quinnanie Shale (Teichert 1950, p. 1791) of the Minilya Sub-Group; Byro Group (Condon 1967, p. 163). Stratigraphic sections of the Quinnanie Shale have been provided by Teichert (1951, p. 117) and Condon (1954, pp. 75-78). The age of the Quinnanie Shale, from its stratigraphic position, is Late Baigendzinian (Late Artinskian, Early Permian). Correlations of the Carnarvon Basin Permian succession with other Australian Permian sequences are given by Dickins (1976). The substage name Baigendzinian is used in the sense of Waterhouse (1978) and Furnish (1973) to designate faunas of Late Artinskian and pre Kungurian (or pre Roadian = early Kungurian) age. This usage, discussed fully by Waterhouse (1978), differs from earlier Soviet usage based on ammonoid studies which included the Kungurian within the Baigendzinian.

Ecology

Specimens of *Lingula* from the Quinnanie Shale, examined by the author, are preserved in rock samples ranging in lithology from siltstone to silty fine sandstone. Many specimens are isolated valves, indicating a degree of post-mortem transport, nevertheless, rare conjoined shells do occur in the collections. The associated fauna is moderately diverse; with eleven genera of molluscs (Dickins 1963) and other brachiopods, including such genera as *Neochonetes, Cancrinella, Spirelytha* and *Fusispirifer.*

Condon (1954, p. 78) considered the Quinnanie Shale to be a "typical" euxinic facies (pyritic black shale) deposited in a barred basin with restricted circulation, sentiments supported, in part, by Thomas (1958, p. 28).

The lithology of the Quinnanie Shale is typical of the sediment occupied by living lingulids (Chuang 1961, Paine 1970, Emig *et al.* 1978). Earlier investigators (e.g. Craig 1952) stressed a muddy environment whereas Emig *et al.* (1978) demonstrated that living lingulids show a clear preference for very fine sand. Chuang (1961) considered that the presence of organic matter in the sediment was to the advantage of lingulids, presumably to provide nutrients.

Since lingulids of the Quinnanie Shale occur as isolated valves, resulting faunal associations may be a mixture of adjacent communities and it may be difficult to interpret the significance of such fossil assemblages (Craig 1952, p. 119). However, the few intact shells are important since Ferguson (1963, p. 672) stated "the possibility of intact shells of this inarticulate brachiopod being transported any appreciable distance is remote". Furthermore Bretsky (1969, p. 52) considered that the Linguloid-Molluscan assemblage, found in the nearest shore environment, was a stable association from Late Ordovician to Late Permian. His observations appear valid for the Quinnanie Shale and presumably transport has not been significant. The Quinnanie Shale contains a species of *Fusispirifer*, the population of which includes a high percentage (60% +) of juvenile individuals as determined from a study of the growth lines. Above and below the Quinnanie Shale the Wandagee and Cundlego Formations represent well aerated sedimentary environments and each contains a diverse, articulate brachiopod dominated fauna. Populations of *Fusispirifer* in each unit consist of 25 and 30% juvenile individuals. The larger proportion of juvenile individuals of *Fusispirifer* in the Quinnanie Shale appears abnormally high, suggesting a high mortality of juveniles due to unfavourable conditions (cf. discussions by Cloud 1948). A tidal flat environment, subjected to salinity variation such as would be caused by the periodic influx of fresh water which would kill off portion of the community, would be consistent with the high percentage of juvenile specimens of the *Fusispirifer* population and the ecology of most modern lingulids. This phenomenon has been well known for modern lingulid communities since Yatsu (1902, p. 66) quoted the observations of Hatta at Matsubate Inlet, Japan. The tolerance of *Lingula* to periods of lower salinity and confinement is well known, (Lum & Hammen 1962, Hammen *et al.* 1962) although little is known of such tolerance ranges (Ferguson 1963, p. 671).

Taxonomy

Lingulids have maintained a remarkable uniformity and simplicity in shell form through time (Emig *et al.* 1978). The need for caution when delineating modern and fossil species on features such as shell outline and ontogenetic stages has been demonstrated by many authors (Kirkby 1860, Kawaguti 1942, Chuang 1961, 1962, Hammond & Kenchington 1978, Deleers & Pastiels 1952). Internal septa and muscle scars (both reflecting muscle attachment) are important in the classification of the group (Rowell 1965, Pajaud 1977, Emig 1977, 1979). The importance of muscle scars at the generic level is illustrated by *Apsilingula* Williams (1977).

SYSTEMATIC PALAEONTOLOGY

Order LINGULIDA Waagen 1885
Superfamily LINGULACEA Menke 1828
Family LINGULIDAE Menke 1828

DIAGNOSIS: The diagnosis by Rowell (1965, p. H262) is accepted with the minor emendation of Williams (1977, p. 403) that the pseudointerarea is not always developed.

DISCUSSION: The Lingulidae has not been subdivided into subfamilies, but recent investigations (Emig *et al.* 1978, Pajaud 1977) indicate that the presence or absence of internal septa is a criterion for distinguishing relation-

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EXPLANATION OF PLATE 14

All figures ×3.5. All specimens whitened with ammonium chloride. All specimens, other than the Holotype, are Paratypes.

All specimens from the Quinnanie Shale, Carnarvon Basin, Western Australia.

Figures 1-15. *Lingula occidentaustralis* sp. nov.

Fig. 1—Ventral valve, MUGD 5180

Fig. 2—Ventral valve, UWA 88098

Fig. 3—Dorsal valve, MUGD 5183

Fig. 4—Dorsal valve, MUGD 5179

Fig. 5—a, b, c. Ventral, profile and dorsal views of Holotype, MUGD 5181

Fig. 6—Dorsal valve, MUGD 5190

Fig. 7—Ventral valve?, MUGD 5182

Fig. 8—Dorsal valve, MUGD 5178

Fig. 9—Dorsal valve, MUGD 5177

Fig. 10—Dorsal valve, MUGD 5187

Fig. 11—Dorsal valve, MUGD 5185

Fig. 12—Dorsal valve, UWA 88099

Fig. 13—Dorsal valve, MUGD 5188

Fig. 14—Dorsal valve, MUGD 5184

Fig. 15—Dorsal valve?, MUGD 5189

PLATE 14

ships within the family. Since the occurrence of the genus *Glottidia* Dall in deposits of Tertiary age was reviewed by Chuang (1964), *Glottidia*—like genera have been shown to date back to the Early Triassic (Busnardo 1969 and Broglio-Loriga 1968 as discussed by Emig *et al.* 1978) and Late Permian (Rowell 1970, Newell & Kummel 1942). Several Carboniferous lingulids possess two septa in the ventral valve and one in the dorsal valve Graham (1970). New genera of septate lingulids are indicated by variations in the type and arrangement of septa, for example a new Permian genus, with four septa in one valve, is indicated by *Lingula permiana* of Stauffer & Schroyer (1920). Illustrations of *Lingula credneri*, from the Lower Zechstein of the Fore Sudetic Monocline, Poland, given by Klapcinski (1971, p. 101, pl. 5, figs 3-6) indicate that some representatives of the *Lingula credneri* group possess internal, thin septa. It is considered that the septa bearing lingulids can be usefully separated into the Glottidiinae subfam. nov. diagnosed as: Lingulidae possessing septa in one or both valves. The subfamily Lingulinae Menke is restricted to those lingulids with weakly to very strongly impressed muscle scars and lacking internal septa.

Subfamily LINGULINAE Menke 1828

Genus LINGULA Bruguiere 1797

TYPE SPECIES: *Lingula anatina* Lamarck; I.C.Z.N. pending.

DIAGNOSIS: As given by Rowell (1965).

DISCUSSION: Rowell (1964, pp. 222-224) has discussed fully the need for the I.C.Z.N. to rule to preserve the stability of the generic name.

Lingula occidentaustralis sp. nov.

Pl. 14, figs 1-15

MATERIAL: A collection of 12 measured specimens and many fragments from locality W.L. 7-"*Lingula* Stage, Wandagee Series, Third *Lingula* Horizon Coolkilya Flat, 44 chains south of Garden Road, 231 Links past Station VIII". Collector C. Teichert. Specimens housed in Geology Department, University of Melbourne (M.U.G.D.). A collection of 11 specimens from locality WL13 (U.W.A. Collection Number 27076), Locality unknown, "*Lingula* Zone" collected by C. Teichert 1940. Specimens housed in Department of Geology, University of Western Australia (U.W.A.).

DIAGNOSIS: Elongate species with lateral margins of shell almost straight and parallel in mature individuals. Muscle scars weakly impressed.

DESCRIPTION: Almost equivalve, biconvex shell. Convexity low; greatest posterior of midlength. Ventral valve slightly extended at umbo, slight development of ventral groove for passage of pedicle. Length almost twice width. Valves similar externally with fine subconcentric growth lines. Interior of valves similar with extremely weakly impressed muscle scars. Dorsal valve interior with broad, linear, medianly placed, gently raised ridge. Ventral valve with similar platform, though narrower. Lateral margins of shell almost straight and parallel in larger specimens.

TABLE 1

MEASUREMENTS OF *Lingula occidentaustralis*. sp. nov.

Specimen No.	Length	Maximum Width	Height	Valve
MUGD 5178	14.8	8.9	1.7	Dorsal
MUGD 5179	13.5	7.7	1.3	Dorsal
MUGD 5180	12.5e	6.6	1.2	Ventral
MUGD 5181*	11.5e	6.5	2.8 (Thickness)	Complete Shell
MUGD 5182	–	7.8	1.7	Ventral?
MUGD 5183	14.2	7.7	1.3	Dorsal?
MUGD 5184	–	7.5	–	Dorsal
MUGD 5185	14.2	7.5	1.4	Dorsal
MUGD 5186	–	7.2	1.3	Dorsal
MUGD 5187	11.1	6.5	–	Dorsal
MUGD 5188	13.8	8.2	–	Dorsal
MUGD 5189	13.1	7.3	1.6	Dorsal
UWA 88098	13.6	7.7	1.4	Ventral
UWA 88099	12.4	7.2	1.2	Dorsal

e – estimate * – holotype

MEASUREMENTS: Measurements (in mm) are given in Table 1. Estimates of the shell length are made from a study of ontogeny of the species when the anterior margin of the shell is damaged.

DISCUSSION: *Lingula occidentaustralis* is similar to several other Permian lingulids, characterised by low, rounded umbones, straight, parallel sides to the shell in old age, and a low, broad median dorsal ridge. *Lingula arctica* Miloradovich (1936) from the early Permian (probably early Kungurian) of Novaya Zemlya (*non* L. *arctica* Wittenburg 1910, from the Lower Triassic of Spitzbergen) is similar, differing in being slightly more quadrate in outline and in possessing muscle scars that are more clearly impressed than those of the Western Australian species. Miloradovich's species was renamed *Lingula*? *miloradovichi* by Ifanova (1972). Her additional material from the Kungurian Vorkut Suite of the Pai-Khoy, while being close in outline to the Western Australian species possesses very strongly impressed muscle scars, recalling the genus *Apsilingula* Williams, 1977, although a muscle arrangement different to that of *Apsilingula* is indicated by Ifanova's figures (Ifanova, 1972, pl. 1, figs 1-7). *Lingula* cf *arctica*: Harker & Thorsteinsson (1960, p. 49, pl. 15, fig. 12) is also close to the Western Australian species, with respect to shell outline, as is *L. freboldi* Gobbett (1964, p. 44, pl. 1, figs 1-2) from the Kungurian to Early Kazanian Upper Brachiopod Chert of Spitzbergen. Closer comparison of the Western Australian species with the Canadian and Spitzbergen species is regrettably impossible as these boreal occurrences are only documented by one or two figures and internal muscle scars are poorly known. Comparison with *L. arctica* Miloradovich from the lower part of the Tumarin Suite, of possible early Kungurian age, from the Western and Northern Verchoyansk (Andrianov, 1966, p. 80) is impossible as the specimens are not figured. *Lingula taimyrensis* Einor (1946, p. 14, pl. 3, figs. 1-3; in the form *L. credneri* var. *taimyrensis*) from the Early Permian (Kungurian?) of the Taimyr Peninsula, is also similar to *L. occidentaustralis* in its subparallel lateral margins, low umbones and internal dorsal ridge, but again the boreal species is poorly known. *Lingula* has been widely recorded from the boreal region with all reports indicating species that are morphologically similar if not identical. The boreal species are also of similar early Kungurian age. The present record of a species of *Lingula* from the late Baigendzinian of Western Australia, that is morphologically similar to the boreal species, provides yet another example of the disjunct geographical distribution of Permian brachiopods that has been discussed by many authors (e.g. Ustritsky 1974).

The group of boreal lingulids outlined above is readily distinguished from most Carboniferous lingulids, which possess a more elliptical outline (Graham 1970, Kalashnikov 1970, Vangerow 1959) and the *L. credneri* group of Permian lingulids, which are much smaller in size and elliptical in outline (Alexandrowicz & Slupczynski 1970).

Asian and central north American lingulids attributed to *Lingula*, as summarised in Table 2, also appear elliptical in outline.

PALAEOGEOGRAPHY AND PALAEOECOLOGY OF PERMIAN LINGULIDAE

Taxonomic Problems

Generic placement of a lingulid species requires an accurate knowledge of internal structures, so generic assignment of many of the species in Table 2 is uncertain. I have restricted the review of Permian lingulids to reports accompanied by illustrations except for the Asian region where records of Permian lingulids are even more poorly documented than accounts for other regions. It is arguable that one or two occurrences listed in Table 2 are Late Carboniferous—as indicated.

Palaeoecology

Ecological distribution of modern lingulids is well documented (Emig *et al.* 1978). They are adapted to shallow marine waters, subject to salinity fluctuations (Plaziat *et al.* 1978). They show a preference for a fine sandy substrate and are restricted by the 8°-10°C isotherms. Emig *et al.* (1978) considered these restrictive parameters constant from the Triassic to the Recent.

The lithology containing Permian forms has seldom been recorded in detail. However, where available, most information indicates a fine sandy lithology (Rowell 1970, Alexandrowicz & Slupczynski 1970, Alexandrowicz & Jarosz 1971). Trechmann (1925, p. 538) recorded specimens of *L. credneri* from a thin bed of yellow dolomitic marl with sand and small rounded pebbles. Yochelson (1968) and Branson (1930) recorded specimens from shales of the Phosphoria Formation of Wyoming. Dickins & Shah (1977, p. 10) recorded lingulids and plant remains from ferruginous sandstones of Badhaura, India.

Several Permian lingulids lived in marine waters subject to fluctuations in salinity. "*Lingula*" *permiana* Stauffer & Schroyer (1920) from the Dunkard Series, Ohio occurs with a marginal marine assemblage. Miloradovich (1936, p. 78) writing of the Permian succession of the south island of Novaya Zemlya noted that "the petrographic character of rocks as well as numerous findings of *Lingula* . . . and plant remains permit to suppose . . . lateral marine deposits". Other records of Permian lingulids demonstrate more normal marine waters by an association of a diverse, articulate brachiopod dominated assemblage (Harker & Thorsteinsson 1960, pp. 10-12).

Palaeogeography and Palaeotemperature Tolerance

The provincialism observed in modern lingulids (Fig. 1) can be readily explained by taking into account the restriction to mobility imposed by the 8°-10°C isotherms. Lower temperatures appear to impose restrictions on the duration of the breeding season of modern lingulids (Chuang 1959). A striking departure from the latitudinal limitations of modern forms is evident in the figures of Permian lingulid distribution (Figs 2 & 3). Similar variations were noticed for Mesozoic and Tertiary members of the Lingulidae by Emig *et al.* (1978) who explained such changes as the result of periods of more equitable warm climates of global extent. Lingulids were widespread during the Permian (Figs 2 & 3) and several of the occurrences are in areas where the waters were cool as indicated by the rock record. While global fluctuations of temperature during the Permian are well known (see for example discussions in Frakes 1979, Waterhouse 1978, Waterhouse & Bonham-Carter 1975) and the alternation of cool and warm water faunas may occur within a single stratigraphic column, the inference is made that the various occurrences discussed below do indicate a tolerance by Permian lingulids of cooler water than is demonstrated by the group today. Never-

TABLE 2

PERMIAN LINGULIDAE OF THE WORLD

SPECIES NAME	AUTHOR	LOCALITY	STRATIGRAPHIC HORIZON	AGE	GENERIC POSITION	ADDITIONAL REFERENCES and NOTES
L. imbituvensis	Oliveira, 1930 (p.18; fig. top left of plate)	Santa Catharina, Brazil	Serie Itarare	Early Permian, Early Sakmarian	Type species of Langella Mendes 1961	Additional figures given by Lange, (1952, p.83; pl. 4, figs. 1-8)
L. budoensis	Martins, 1948 (p.237; figs. 1-2)	Rio Grande do Sul, Brazil	Serie Marica	Early Sakmarian	Langella	Synonymised with L. imbituvensis by Lange (1952) and Mendes (1961)
L. exporrecta	Girty, 1910 (p.22; pl.1, fig.1)	Thomas Fork Wyoming U.S.A.	Phosphate Beds of Park City Formation	Artinskian-Kungurian	Lingula	
L. carbonaria	Girty, 1910 (non Shumard 1858?; pp.20-22, pl.1, figs.2-5)	"	"	"	Lingula	Lingula carbonaria Shumard 1858, p.215 is a Pennsylvanian species
L. sp, cf. carbonaria	Yancey, 1978 (p.280, pl.1, fig.1)	Butte Mts Nevada, U.S.A.	Loray Formation	Kungurian	Lingula	
Lingula sp.	Cooper, 1957 (pl.1A, figs.1-3)	Oregan U.S.A.	Coyote Butte Formation	Kungurian	Lingula	
L. permiana	Stauffer and Schroyer 1920 (p.143; pl.9, figs.1-5)	Ohio U.S.A.	Dunkard Series (in black Shales of Washington Coal)	Early Permian	New genus of subfamily Glottidiinae	The presence of four septa in one valve indicates a new genus related to Glottidia
L. borealis	Newell and Kummell 1942 (p.953; pl.2, figs.1-4)	Wyoming Idaho Montana U.S.A.	Dinwoody Formation	Latest Permian	Glottidia	Relationship to L. borealis Bittner 1899 requires examination
L. cf. arctica	Harker and Thorsteinsson 1960 (p.49, pl.15, fig.12)	Grinnell Pen. Devon Island Arctic Canada	Assistance Formation	Kungurian	Lingula	H. and T. compared their specimens with L. arctica Miloradovich 1936, not L. arctica Wittenburg 1910 (p.37, pl.1, fig.7)
L. ovata	Oana, 1847 (p.152)	Black Head, Sydney Basin Australia	Sandstones of Gerringong Volcanics	Kazanian	Lingula?	Dana 1849, (text p.655-656, Atlas pl.2, fig.6)
L. mytiloides (non L. mytiloides Sowerby 1813)	Etheridge 1892 (p.264, pl.13, fig.19)	Spring Creek Cania, Bowen Basin. Australia	Yarrol Formation ?	Sakmarian ?	Lingula	Occurs with small Permian assemblage (Reid, 1930, p.60). Not mentioned by Dear (1968) Stratigraphic position unclear.
L. occidentaustralis	Herein	Carnarvon Basin. Western Australia	Quinnanie Shale	Late Artinskian, Baigendzhinian	Lingula	
L. scrutata	Reed, 1931 (p.39; pl.6, figs.6-7)	Salt Range Pakistan	Amb Formation	Artinskian	Lingula?	Rowell (1970, p.111 discusses stratigraphic position
L. cf. borealis	Rowell, 1970 (p.113; pl.1)	Salt Range Pakistan	Kathwai Member	Latest Permian	Glottidia?	The presence of internal septa indicates a member of the Glottidiinae
L. aff. atra	Schellwien, 1911 (p.141; pl.1, fig.4)	Sin-ho-yi China	?	Gzhelian or Assellan	Lingula	L. atra Herrick (1888, p.16, pl.10, fig.30) is an Early Carboniferous species
Lingula sp.	Wang, 1977 (p.399, figs. 1-2)	Weishan Lake Jiangso Province China	Shangshihezi Formation	Permian	Lingula	
L. credneri	Grabau, 1924 (p.497)	Ta-Lai-Pai Hung, Shui-Hsien China	Shansi Series	Late Permian, Kazanian	?	Not figured. L. credneri Geinitz is discussed below
Lingula sp.	Patte, 1935 (p.14-15, pl.1, fig.3)	Lon feng ya Kueichow, China	?	Latest Permian or Triassic	Lingula	
Lingula sp.	Masslenikov 1950 (p.102)	Sikhote Alin	Sandstone, Limestone Suite	Early Permian	-	Not figured

TABLE 2—(*continued*)

SPECIES	AUTHOR	LOCALITY	STRATIGRAPHIC HORIZON	AGE	GENERIC POSITION	ADDITIONAL REFERENCES and NOTES
L.kolymaensis	Zavodovsky,1968 (p.70,pl.30, fig.3)	Kolyma Basin N.E. Siberia	Burgaliisk Suite	Asselian	Lingula	Also figured by Zavodovsky and Stepanov (1971,p.70; pl.1. figs.2-3). May be middle to late Carboniferous (Ustritsky and Muromtseva 1973, p.117)
L.taimyrensis	Einor, 1946 (p.14; pl.3, figs.1-3)	Taimyr Peninsula	Lower Permian	Early Permian	Lingula	
L.miloradovichi	Ifanova,1972 (p.77; pl.1 figs.1-7)	Pai-Khoy Pechora Basin	Vorkut Suite	Kungurian	Lingula	Ustritsky 1960 (p.94; pl.1, figs.1-2)
= L.arctica	Ustritsky,1960	" "				
= L.arctica (non L.arctica Wittenburg,1910)	Miloradovich, 1936	Mezhdusharsky Island Novaya Zemlya	Lower Permian	Early Permian	Lingula	Miloradovich 1936 (p.37, pl.2, fig.4; pl.3, figs.1-3)
L.praeorientalis	Ifanova,1972 (p.79, pl.1; figs.8-9)	Pai Khoy	Gusinaya Suite	Early Artinskian	Lingula	
L. hyberborea = L.crednerl Ustritsky 1960	Ifanova,1972 (p.80, pl.1; figs.10-16)	Pai Khoy	Vorkut Suite	Kungurian	Allied to Glottidia?	Ifanova (p.1; fig.15) indicates the presence of septa. Ustritsky 1960 (p.96; pl.1, figs.3-6)
L. vorkutana	Ifanova,1972 (p.81; pl.1, figs.17-19)	Pai Khoy	Vorkut Suite	Kungurian	Lingula	
L.rotundata	Pogorevitch and Ifanova; Ifanova 1972 (p.82; pl.1, fig.20)	Pai Khoy	Vorkut Suite	Kungurian	?	May not be a lingulid
L. squamiformis (non L.squamiformis Phillips, 1836)	Ustritsky and Chernyak 1963 (p.67; pl.1, fig.1)	Taimyr Peninsula	Makarovsk Horizon	Late Permian	Lingula	L.squamiformis Phillips (1836, p.221; pl.11; fig.14) is Early Carboniferous in age
Lingula orientalis	Golovkinsky,1868 (p.360; pl.2; figs.11-12)	Schiya River	Kazanian	Kazanian	Lingula	
Lingula lawrskyi	Necaev,1894 (p.139;pl.6; figs.11-12)	Kazan River	Kazanian	Kazanian	Lingula	
Lingula sp.	Grushenko,1975 (pl.25; figs.2-3)	Donetz Basin	Nikitov and Kalitvenskaya suites	Asselian	Lingula	
Lingula freboldi	Gobbett,1964 (p.44,pl.1; figs.1-2)	Spitzbergen	Upper Brachiopod Chert	Kazanian	Lingula	
Lingula credneri	Geinitz,1848 (p.11;pl.4; figs.23-24)	Germany	Zechstein (Kupferschiefer)	"	Lingula	Geinitz,1861 (p.106;pl.8, fig.1q;pl.15,figs.12-13)
"	King,1850(p.83; pl.6,figs.25-27) Davidson,1858 (p.51,pl.4, figs.30-31)	England "	Marl-Slate & Lower Magnesian Limestone	"	Lingula	
"	Alexandrowicz and Slupizynski 1970,(p.700; pls.1 and 2)	West Poland	Lower Zechstein	Kungurian	Lingula	
"	Alexandrowicz and Jarosz 1971 (figs.1-6)	"	Sandstones			
"	Necaev,1894 (p.138;pl.5; fig.20)	Viatka River	Kazanian	Kazanian	Lingula	

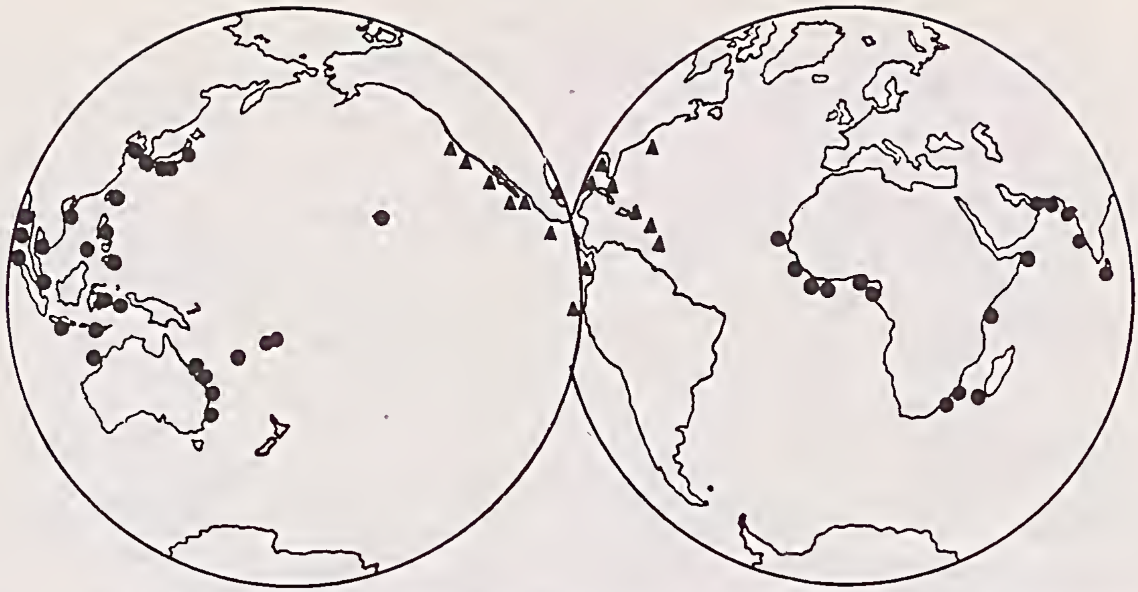

FIG. 1—The distribution of modern lingulids. • = *Lingula;* ▲ = *Glottidia.* Based on Zezina 1970, p. 155 and Emig *et al.* 1978, fig. 9.

theless in order to confirm this broader temperature tolerance detailed descriptions of the immediately associated stratigraphic sequence and lithology is required. Such information is invariably lacking. The South American occurrences are found in a stratigraphic interval at least in part of glacigene origin—the Itarare Series, Santa Catarina, Brazil, (Ruedemann 1929). *Lingula*? *ovata* Dana (1847-1849) from the Sydney Basin, Eastern Australia occurs in the sandstones of the Gerringong Volcanics and came from Black Head where the lithology is a sandstone with numerous glacigenic dropstones. Boreal occurrences also indicate cool to cold water. Miloradovich (1936, p. 78) indicated a glacigene component in the early Permian sequence of Novaya Zemlya. Other Boreal occurrences (e.g. Ifanova 1972, Einor 1946, Zavodovsky 1968) are with faunas of low diversity indicating cool to cold water (Waterhouse & Bonham-Carter 1975).

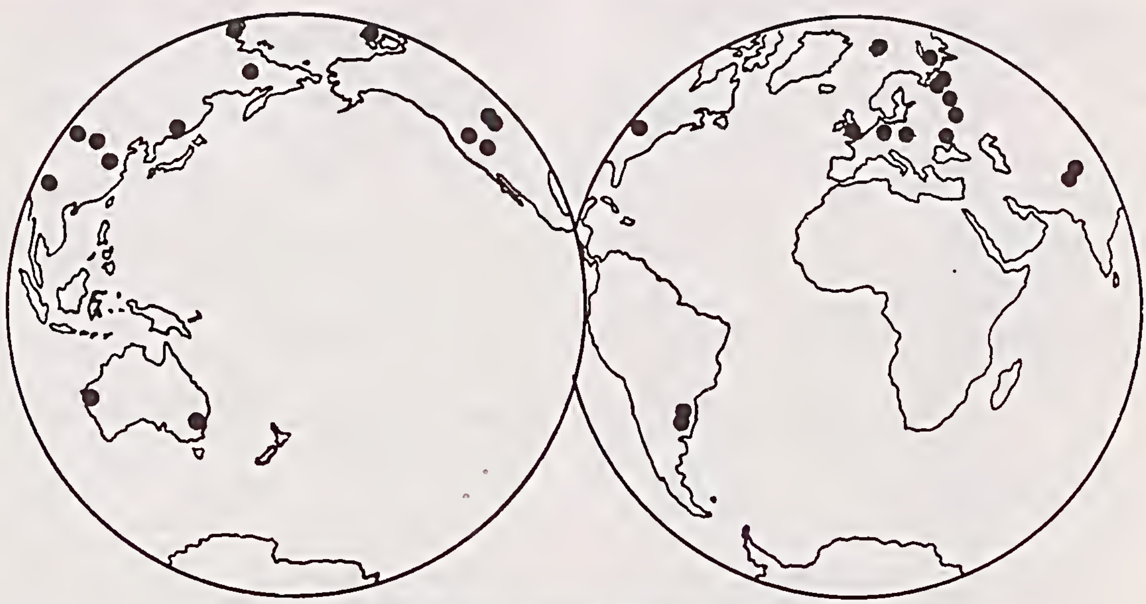

FIG. 2—The distribution of Permian lingulids on the modern globe.

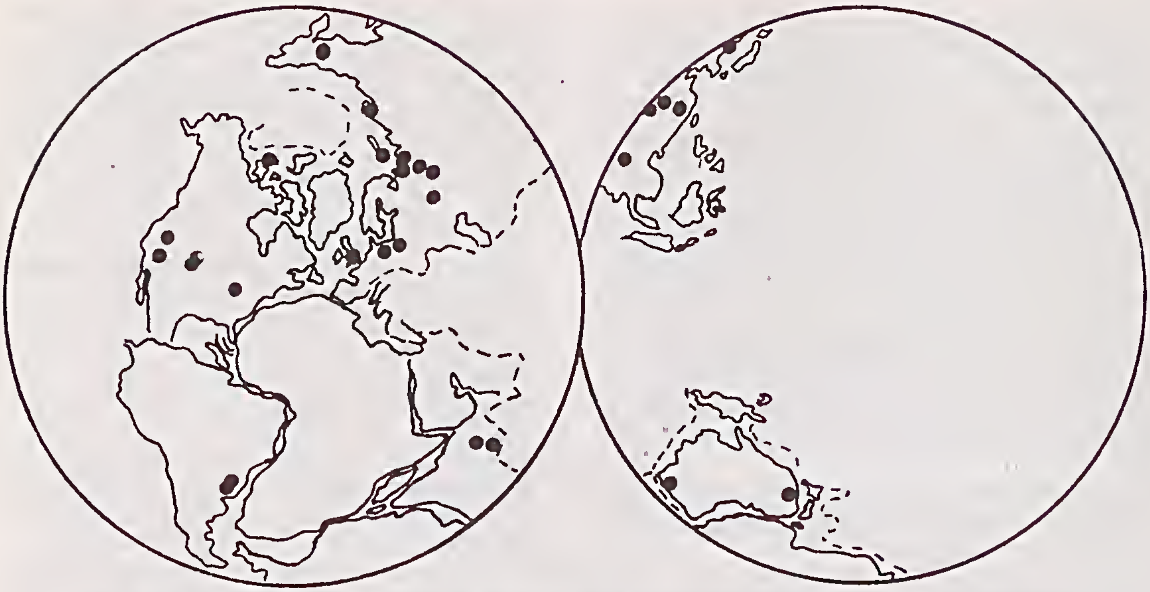

Fig. 3—The distribution of Permian lingulids on a Permian reconstruction of the continents.

Projection of Maps

Figures 1, 2 and 3 utilize the Lambert Equal-Area projections of Briden *et al.* (1974). Although a complete review of all reconstructions is beyond the scope of the present review, it should be noted that the Permian reconstruction of Briden *et al.* is only one of many available. Many palaeontologists have criticised this particular model as inconsistent when compared with the distributions of their faunas and floras (e.g. Hart 1974, using palynofloras; Waterhouse & Bonham-Carter 1975, using brachiopods; Ross 1979, using fusulinids and Ziegler *et al.* 1977, summarizing several groups). Palaeomagnetic data appear equivocal, with Japanese data indicating a Permian position at 13°N. (Minato & Fujiwara 1965) and/or an equatorial position (Hattori & Hirooka 1979) while Malaysian data indicate a Permian position at 15°N (McElhinny *et al.* 1974), unless the Asian plate (or plates) has rotated, as suggested by Hart (1974, p. 156). Other investigations, documenting stratigraphic or structural relationships, have indicated the close proximity of South East Asia to Gondwana (e.g. Ridd 1971, Acharyya 1979, Zonenshayn & Gorodnitsky 1977), unlike the Briden *et al.* model.

The Briden *et al.* (1974) and the Scotese *et al.*(1979) models are consistent with the recent review of the tectonics of China (Huang 1978), from a plate tectonics viewpoint.

CONCLUSIONS

The distribution of Permian lingulids indicates an adaption to variable water chemistry and fine sandy sediment, similar to living forms. A wider tolerance of temperature variations, than that shown by modern species, is also indicated, with species inhabiting both warm (Asia) and cool (Eastern Australia, South America, Northern U.S.S.R. and Northern North America) water realms. Earlier in the Palaeozoic lingulids appear, at times, to have been further removed from their modern constraints, certainly occurring frequently in deeper water (Cherns 1979), or in a wide variety of sediment types such as muds, silts, ironstones, limestones and coarse sands (Graham 1970, p. 170). The above discussion indicates warnings against the assumption that a long-lived genus (or family) may occupy the ecological niche now that it has always occupied and that it may be still limited by the same set of ecological constraints. The family Lingulidae appears to have become more restricted (specialized?) through time; for example in relation to temperature since the Permian, and lithology since the Carboniferous.

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REFERENCES

ACHARYYA, S. K. 1979. India and Southeast Asia in Gondwanaland fit. *Tectonophysics* 56: 261-276.

ALEXANDROWICZ, S. W., & JAROSZ, J., 1971. Palaeoecology of the Zechstein *Lingula* sandstones from Lubin (West Poland). *Bull. Acad. pol.‾Sci. Ser. Sci geol. geogr.* 19: 183-191.

————, & SLUPCZYNSKI, K., 1970. On the presence of *Lingula credneri* Geinitz in the Lower Zechstein deposits in the vicinity of Ostrow Wielkopolski. *Acta geol. pol.* 20: 693-707.

ANDRIANOV, V. N., 1966. *Verkhnepaleozoiskie otlozheniya Zapadnogo Verkhoyan'ya.* "Nauka". Novosibirsk.

BRANSON, C. C., 1930. Paleontology and stratigraphy of the Phosphoria Formation. *Univ. Mo. Stud.* 5(2): 1-99.

BRETSKY, P. W., 1969. Evolution of Paleozoic benthic marine invertebrate communities. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 6: 45-59.

BRIDEN, J. C., DREWRY G. E. & SMITH, A. G., 1974. Phanerozoic Equal-Area world maps. *J. Geol.* 82: 555-574.

BROGLIO-LORIGA, C. 1968. Alcune considerazioni su *Lingula tenuissima* Bronn del Werfeniano delle dolomiti. *Ferrara Universita degli studi Annali. Sez. 9. Sci. geol. e paleontol.* 4(12): 189-202.

BUSNARDO, R., 1970. Faunules du Trias subbetique (Andalousia). *Lyon Univ. Doc. Lab. geol. Fac. Sci.* 37: 55-84.

CHERNS, L., 1979. The environmental significance of *Lingula* in the Ludlow Series of the Welsh Borderland and Wales. *Lethaia* 12: 35-46.

CHUANG, S. H., 1959. The breeding season of the brachiopod *Lingula unguis* (L.). *Biol. Bull. mar. biol. Lab., Woods Hole*, 117: 202-207.

————, 1961. Growth of the postlarval shell in *Lingula unguis* (L.) (Brachiopoda). *Proc. zool. Soc. Lond.* 137: 299-310.

————, 1962. Statistical study of variations in the shell of *Lingula unguis* (L.) *Vidensk. Meddr. dansk naturh. Foren.* 124: 199-215.

————, 1964. The affinity of *Lingula dumortieri* Nyst with *Glottidia. J. Paleont.* 38: 155-157.

CLOUD, P. E., 1948. Assemblages of diminutive brachiopods and their paleoecological significance. *J. sedim. Petrol.* 18: 56-60.

CONDON, M. A., 1954. Progress report on the stratigraphy and structure of the Carnarvon Basin, Western Australia. *Rep. Bur. Miner. Resour. Geol. Geophys. Aust.* 15: 1-163.

————, 1967. The Geology of the Carnarvon Basin, Western Australia. Part 2. Permian Stratigraphy. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* 77: 1-191.

COOPER, G. A., 1957. Permian Brachiopods from Central Oregon. *Smithson. Misc. Collns.* 134(2): 1-79.

CRAIG, G. Y., 1952. A comparative study of the ecology and palaeontology of *Lingula. Trans. Edinb. geol. Soc.* 15: 110-120.

DALL, W. H., 1870. A revision of the Terebratulida and Lingulidae. *Am. Jour. Conchol.* 6: 88-168.

DANA, J. D., 1847. Descriptions of Fossil Shells of the Collections of the Exploring Expedition under the command of Charles Wilkes, U.S.N. obtained in Australia. *Am. J. Sci* (2)4: 151-160.

————, 1849. Fossils of New South Wales, *in United States exploring expedition. During the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes U.S.N.*, Vol. 10. Geology. Appendix 1. Part 1., 681-720. C. Sherman. Philadelphia.

DAVIDSON, T. 1858. A Monograph of the British fossil Brachiopoda. Vol. 2(4). The Permian Brachiopoda. *Palaeontograph. Soc. Monogr.* 1-274.

DEAR, J. F., 1968. The geology of the Cania District. *Publ. Geol. Surv. Qld.* 330: 1-27.

DELEERS, C. & PASTIELS, A., 1952. Contribution a L'etude biometrique de *Lingula mytiloides* Sowerby du Westphalien de la Belgique. *Assoc. Etude. Paleont. Strat. Houilleres. Publ.* 12: 1-67.

DICKINS, J. M., 1963. Permian pelecypods and gastropods from Western Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* 63: 1-203.

————, 1976. Correlation Chart for the Permian System of Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* 156B: 1-26.

————, & SHAH, S. C., 1977. Correlation of the Permian Marine sequences of India and Western Australia. *4th Int. Gondwana Symp. Calcutta. Key Paper*, 1-44.

EINOR, O. L., 1946. Brachiopods from the Lower Carboniferous and Lower Permian of west Taimyr. *Trudy Gorno-Geologicheskogo Upravleniya* 26.

EMIG, C. G., 1977. Reflexions sur la taxonomic des especes due genre *Lingula* (Brachiopodes, Inarticules). *C.r. hebd. Seanc Acad. Sci. Paris* 285D: 523-525.

————, 1979. Three *Lingula* of the Queensland coast. *Mem. Qld. Mus.* 19: 381-391.

————, GALL, J., PAJAUD, D. & PLAZIAT, J., 1978. Reflexions critiques sur l'ecologie et la systematique des lingules actuelles et fossiles. *Geobios* 11: 573-609.

ETHERIDGE, R. JR., 1892. *In* JACK, R. L., & ETHERIDGE, R. JR., Geology and Palaeontology of Queensland and New Guinea *Publ. Geol. Surv. Qld.* 92, 2 vols.

FERGUSON, L., 1963. The paleoecology of *Lingula squamiformis* Phillips during a Scottish Mississippian marine transgression. *J. Paleont.* 37: 669-681.

FRAKES, L. A., 1979. *Climates throughout Geologic Time.* Elsevier Amsterdam.

FURNISH, W. M., 1973. Permian Stage Names. *Mem. Can. Soc. Petrol. Geol.* 2: 522-548.

GEINITZ, H. B., 1848. Die versteinerungen des deutschen Zechsteingebirges. In GEINITZ, H. B. & GUTBIER, A. von (Eds.), *Die versteinerungen des Zechsteingebirges und Rothliegenden oder des Permischen Systemes in Sachsen.* Heft 1, 1-26. Arnoldische Buchhandlung. Dresden und Leipzig.

————, 1861. *Dyas oder die Zechsteinformation und das Rothliegende.* Heft 1. Die animalischen ueberreste der Dyas, 1-130. Englemann. Leipzig.

GIRTY, G., 1910. The fauna of the Phosphate beds of the Park City Formation in Idaho, Wyoming and Utah. *Bull. U.S. geol. Surv.* 436: 1-81.

GOBBETT, D. J., 1964. Carboniferous and Permian brachiopods of Svalbard. *Skr. norsk. Polar inst.* 127: 1-201.

GOLOVKINSKY, N. A., 1868. O Permsko formatsii v tsentral'noi chasti Kamsko-Volzhskago Basseina. *Materialy dlya geologii Rossii,* 1: 273-415.

GRABAU, A. W., 1924. *Stratigraphy of China. Part 1. Palaeozoic and Older.* Geol. Surv. China. Peking.

GRAHAM, D. K., 1970. Scottish Carboniferous Lingulacea. *Bull. geol. Surv. Gt. Br.* 31: 139-184.

GRUSHENKO, N. V., 1975. Brakhiopody nizhnei permi i ix znachenie dlya stratigrafii Vostochno—Ukrainskogo nefterazonosnogo basseina. In *Stratigr. verkhn. paleozoya i nizhn. mesozoya Deneprovsko—Donetsk bpadniy*, 83-118. "Nedra". Moscow.

HAMMEN, C. S., HANLON, D. P. & LUM, S. C., 1961. Oxidative metabolism of *Lingula. Comp. Biochem. Physiol.* 5: 185-191.

HAMMOND, L. S. & KENCHINGTON, R. A., 1978. A biometric case for revision of the genus *Lingula* (Brachiopoda, Inarticulata) from Queensland, Australia. *J. Zool. Lond.* 184: 53-62.

HARKER, P. & THORSTEINSSON, R., 1960. Permian rocks and faunas of Grinnell Peninsula, Arctic Archipelago. *Mem. geol. Surv. Brch. Can.* 309: 1-89.

HART, G. F., 1974. Permian palynofloras and their bearing on Continental Drift. *In* Ross, C. A. (Ed.), Paleogeographic Provinces and Provinciality. *S.E.P.M. Spec. Pub.* 21: 148-164.

HATTORI, I. & HIROOKA, K., 1979. Paleomagnetic results from Permian greenstones in central Japan and their geologic significance. *Tectonophysics* 57: 211-235.

HERRICK, C. L., 1888. Geology of Licking County. Part IV. List of Waverly Fossils, Continued. *Bull. Scient. Labs. Denison Univ.* 4: 11-123.

HUANG, C. C., 1978. An outline of the tectonic characteristics of China. *Eclogae geol. Helv.*, 71: 611-635.

IFANOVA, V. V., 1972. Permian brachiopods of the Pechora Basin. *In* IFANOVA, V. V. and SEMENOVA E. G. (Eds) *Middle Carboniferous and Permian brachiopods from East and North of the European part of the USSR*, 72-161. Izd-vo Nauka. Moscow.

KALASHNIKOV, N. V., 1970. O bezzamkovykh brakhiopod Karbona Severnogo Urala i ikh ekologii. In, *Fauna i Flora paleozoya Severo-Vostoka Evropeiskoi chasti SSSR*, 5-15. Izdvo "Nauka" Leningrad.

KAWAGUTI, S., 1943. A biometrical study on *Lingula unguis. Venus*, Kyoto, 12: 171-182.

KING, W., 1850. A monograph of the Permian fossils of England. *Palaeontograph. Soc. Monogr.* 1-258.

KIRKBY, J. W., 1860. On the occurrence of *Lingula credneri* Geinitz in the coal measures of Durham. *Q. Jl geol. Soc. Lond.* 16: 412-420.

KLAPCINSKI, J., 1971. Litologia, fauna, stratigrafia i paleogeografia Permu monakliny Przedsudeckiej. *Geologia Sudetica, Warszawa* 5: 77-136.

LANGE, F. W., 1952. Revisao da faunula marinha do folhelho Passinho. *Dusenia* 3: 81-91.

LUM, S. C. & HAMMEN, C. S., 1964. Ammonia excretion of *Lingula. Comp. Biochem. Physiol.* 12: 185-190.

MARTINS, E. A., 1948. Fosseis marinhos na serie Marica, Rio Grande de Sol. *Minerac. Metall.* 12(71): 237-239.

MASSLENIKOV, D. F., 1950. K faune permskikh otlozhenii yugo-vostoka SSSR. *Trudy vses. nauchno-issled. Geol. Inst.* 1:100-114.

MCELHINNY, M. W., HAILE, N. S. & CRAWFORD, A. R., 1974. Palaeomagnetic evidence shows Malay Peninsula was not a part of Gondwanaland. *Nature* 252: 641-645.

MENDES, J. C., 1961. *Langella*, Novo genero de Lingulideo de Serie Subarao. *Parana Univ. Bol. geol.* 5: 1-8.

MILORADOVICH, B. V., 1936. Lower Permian fauna from the Island Mejdusharsky (southern island of Novaya Zemlya). *Trud. arkt. Inst. Akad. Nauk SSSR* 37: 37-82.

MINATO, M. & FUJIWARA, Y., 1965. Magnetic pole positions determined by the Japanese Palaeozoic rocks. *J. Assoc. Geol. Coll. Japan* 78: 21-22.

NECHAEV, A. V., 1894. Fauna permskikh otlozhenii vostochnoi polosy Europeiskoi Rossii. *Trudy Obshch. Estest. Imp. kazan. univ.* 27(4).

NEWELL, N. D. & KUMMEL, B., 1942. Lower Eo-Triassic Stratigraphy, Western Wyoming and Southeast Idaho. *Bull. geol. Soc. Amer.* 53: 937-996.

OLIVEIRA, E. P. DE, 1930. Fosseis marinhos da Serie Itarare do Estado de Santa Catarina. *Anais Acad. bras. Cienc.*, 2: 17-21.

PAINE, R. T., 1970. The sediment occupied by recent lingulid brachiopods and some paleoecological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 7: 21-31.

PAJAUD, D., 1977. Choix et hierarchisation des caracteres taxinomiques pour la reconnaissance des lingules post-paleozoiques. *Geobios* 10: 961-965.

PATTE, E., 1932. Fossiles paleozoiques et mesozoiques du sud-ouest de la Chine. *Palaeont. sin. Ser. B* 15(2): 1-50.

PHILLIPS, J., 1836. *Illustrations of the Geology of Yorkshire. Part II. The Mountain Limestone District.* J. Murray. London.

PLAZIAT, J.-C., PAJAUD, D., EMIG, C. & GALL J-C., 1978. Environments et distribution bathymetrique des lingules actuelles; consequences pour les interpretations paleogeographiques. *Bull. Soc. geol. Fr.* 20: 309-314.

REED, F. R. C., 1931. New fossils from the *Productus* Limestone of the Salt Range with notes on other species. *Mem. geol. Surv. India Palaeont. Indica N.S.*, 17: 1-56.

REID, J. H., 1927. The Queensland Upper Palaeozoic Succession. *Publ. Geol. Surv. Qld.* 278: 1-96.

RIDD, M. F., 1971. South-East Asia as a part of Gondwanaland. *Nature* 234: 531-533.

ROWELL, A. J., 1964. *Lingula* Bruguiere [1797] (Brachiopoda Inarticulata); proposed designation of a type species under the plenary powers Z, N. (S.) 1598. *Bull. zool. Nom.*, 21: 222-224.

ROWELL, A. J., 1965. Inarticulata. In MOORE, R. C., (Ed.) *Treatise on Invertebrate paleontology. Part H. Brachiopoda.* Vol. 1., H260-H296. Geol. Soc. Amer., Univ. Kansas Press.

———, 1970. *Lingula* from the basal Triassic Kathwai Member, Mianwalia Formation, Salt Range and Surghar Range, West Pakistan. In KUMMEL, B. & TEICHERT, C., (Eds). *Stratigraphic Boundary Problems*, Uni. Kansas Dept. geol. Spec. Publ. 4, 111-116.

ROSS, C. A., 1979. Late Paleozoic collision of North and South America. Geology, 7: 41-44.

RUEDEMANN, R., 1929. Fossils from the Permian tillite of Sao Paulo, Brazil, and their bearing on the origin of tillite. *Bull. geol. Soc. Amer.* 40: 417-426.

SCHELLWIEN, E., 1911. Palaozoische und Triadische Fossilien in Ostasien. In FUTTERER, K., (Ed.), *Durch Asien*. Vol. 3, 125-174. D. Reimer. Berlin.

SCOTESE, C. R., BAMBACH, R. K., BARTON, C., VAN DER VOO, R. & ZIEGLER, A. M., 1979. Paleozoic Base Maps. *J. Geol.* 87: 217-277.

SHUMARD, B. F. & SWALLOW, G. C., 1858. Descriptions of new fossils from the coal measures of Missouri and Kansas. *Trans. Acad. Sci. St. Louis* 1: 198-227.

STAUFFER, C. R. & SCHROYER, C. R., 1920. The Dunkard Series of Ohio. *Bull. geol. Surv. Ohio.* Ser. 4, 22: 1-167.

TEICHERT, C., 1939. Recent research work in the Permian of Australia. *Aust. J. Sci.* 2: 5-7.

———, 1950. Some recent additions to the stratigraphy of Western Australia. *Bull. Am. Ass. Petrol. Geol.* 34: 1787-1794.

———, 1952. Carboniferous, Permian and Jurassic in the Northwest Basin, Western Australia. *19th. Int. Geol. Cong., Symp. Gond.* 115-135.

THOMAS, G. A., 1958. The Permian Orthotetacea of Western Australia. *Bull Bur. Miner. Resour. Geol. Geophys. Aust.* 39: 1-159.

TRECHMANN, C. T., 1921. Some remarkably preserved brachiopods from the Lower Magnesian Limestone of Durham. *Geol. Mag.* 58: 538-543.

USTRITSKY, V. I., 1960. Permskiye brakhiopody Pay-Khoy. *Trudy nauchno-issled. Inst. Geol. Arkt.* 111: 93-130.

———, 1974. O bipolyarnosti faun pozdnego paleozoya. *Paleont. Zhur.* 1974(2): 33-37.

———, & CHERNYAK, G. E., 1963. Biostratigrafiya i brakhiopody verkhnego paleozoya Taimyra. *Trudy naucho-issled. Inst. Geol. Arkt.*, 134: 1-139.

———, & MUROMTSEVA, V. A., 1973. Review: On the field atlas of the Permian fauna and flora of North-East USSR., *Paleont. Jour.* 1973(1): 117-120.

VANGEROW, E. F., 1959. Die fauna des Westdeutschen Oberkarbons. Die inarticulaten Brachiopoden des west deutschen flozfuhrenden Oberkarbons., *Palaeontographica.* Abt. A., 113: 36-60.

WANG, R., 1977. A discovery of *Lingula* sp. in Shangshihezi Formation on the west side of Weishan Lake, Jiangsu Province. *Scient. Geol. Sin.* 1977(4): 399-400.

WATERHOUSE, J. B. 1978. Chronostratigraphy for the World Permian. *Am. Ass. Petrol. Geol. Studies in Geology* 6: 229-322.

———, J. B. & BONHAM-CARTER, G. F., 1975. Global distribution and characters of Permian biomes based on brachiopod assemblages. *Can. J. Earth Sci.* 12: 1085-1146.

WILLIAMS, A. J., 1977. Insight into lingulid evolution from the late Devonian. *Alcheringa* 1: 401-406.

WITTENBURG, P. V., 1910. Uber einige trias fossilien von Spitzbergen. *Trudy geol. Muz. im. Petra Velikogo* 4(2): 31-39.

YANCEY, T. E., 1978. Brachiopods and molluscs of the Lower Permian Arcturus Group, Nevada and Utah. Part 1. Brachiopods, Scaphopods, Rostroconchs and Bivalves. *Bull. Amer. Paleont.* 74(303): 257-367.

YATSU, N., 1902. On the habits of the Japanese *Lingula*. *Annotnes zool. jap.* 4: 61-67.

YOCHELSON, E. L., 1968. Biostratigraphy of the Phosphoria, Park City and Shedhorn Formations. *U.S. geol. Surv. Prof. Pap.* 313D: 571-660.

ZAVODOVSKY, V. M., 1968. Novye vidy permskikh lingulid i distsinid severo-vostoka SSSR. In MARKOVSKII, B. P., (Ed.) *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR.* 2: 70-71. Izd-vo "Nedra". Moscow.

ZAVODOVSKY, V. M. & STEPANOV D. L., 1971. Typ Brachiopoda. In KULIKOV, M. V., (Ed.) *Polevoi atlas permskoi fauny i flory severo-vostoka SSSR*, 70-182. Magadan.

ZEZINA, O. N., 1970. O raspredelinii brakhiopod v sovremennom okeane v suyazi s voprosami zoogeograficheskogo rayonirovaniya. *Paleont. Zh.* 1970(2): 3-17.

ZIEGLER, A. M., SCOTESE, C. R., MCKERROW, W. S., JOHNSON, M. E. & BAMBACH, R. K., 1977. Paleozoic biogeography of continents bordering the Iapetus (Pre-Caledonian) and Rheic (Pre-Hercynian) Oceans. *Milwaukee Public Museum. Spec. Pub. Biol. Geol.* 2: 1-22.

ZONENSHAYN, L. P. & GORODNITSKY, A. M., 1977. Paleo-Mesozoic and Mesozoic reconstructions of the continents and oceans. 2. Late Paleozoic and Mesozoic reconstructions. *Geotectonics* 11: 159-172.